

A silicified wood of Juglandaceae from the Lower Miocene sand and gravel pit at Rauscheröd, East Bavarian Molasse, Germany

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With 8 figures and 3 tables

Abstract

The present paper is in continuation of the systematic study of silicified wood remains collected in Tertiary sediments of Southern Germany, Upper Freshwater Molasse. This paper deals with the first wood of Juglandaceae, comparable to *Carya*, from the sand and gravel pit exposure at Rauscheröd, southeast Bavaria. Minute anatomy: Diffuse porous, in part thick-walled vessels, simple perforations, thin-walled tyloses, apotracheal parenchyma bands, abundant barrel-shaped idioblasts. The present investigation extends our knowledge of the "exotic" fossil wood flora of the locality at Rauscheröd, East Bavarian Molasse, geological age 18.5 million years.

Kurzfassung

Etwa 120 verkieselte Holzreste aus dem Ortenburger Schotter, Fundort Sand- und Kieswerk Rauscheröd bei Passau, wurden bisher anhand von Dünnschliffen xylem-anatomisch identifiziert. In dieser Arbeit wird erstmals das Holz einer Juglandaceae, vergleichbar mit der Gattung *Carya*, beschrieben. Anatomische Merkmale: Zerstreutporig, teils dickwandige Gefäße, einfache Durchbrechungen, dünnwandige Thyllen, schmale apotracheale Parenchymbänder, zahlreiche Idioblasten mit rhomboiden Einzelkristallen. Das Juglandaceen-Holz ergänzt unsere bisherige Kenntnis über die Zusammensetzung der „exotischen“ Holzflora aus Rauscheröd, Alter 18,5 Millionen Jahre.

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Fig. 1. Exposure Rauscheröd showing sediments of 15–20 m height. Sediments above a distinct boundary (dark line) are from the limnic Freshwater Molasse; the Ortenburg Gravel is situated in the underlying strata (Photograph Dr. F. PFEIL).

1. Introduction

In Tertiary sediments from the northalpine Molasse basin thousands of silicified wood pieces have been collected in recent decades. The sand and gravel pits in the southeast of Bavaria have proved to be particularly rich in fossil woods in the Lower Miocene exposure of Rauscheröd close to Passau. The geological age of the Ortenburg Gravel, dated by fossil vertebrates, corresponds to Mammal Neogene zone MN 4b (HEISSIG 1997), more than 18.5 million years ago. In Rauscheröd the silicified woods lie irregularly in large fluvial sediments of the so-called „Ortenburger Schotter“. The silicified wood fragments are frequently rounded and fist-sized but also long rough pieces from broken logs of maximum 7 m length. The Ortenburg Gravel cuts erosionally into Oligo-Miocene sediments that were originally deposited in a near-shore environment at the northern rim of the Paratethys (UNGER 1995, 1997). It also took up marine and brackish fauna and remnants of terrestrial mammals. The Ortenburg Gravel stream was active during the Upper Ottnang time. Its gravel and sand were deposited north of what was left of the Oncophora sea basin in East Lower Bavaria. From 1985 until now, more than 126 silicified wood remains have been described from the exposure at Rauscheröd: Bombacaceae, Ebenaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Lauraceae, Meliaceae and Tiliaceae. This paper deals with the first record of Juglandaceae.

2. Anatomical study

Juglandaceae

Eucaryoxylon MÜLLER-STOLL & MADEL 1960

Type species: *E. crystallophorum* MÜLLER-STOLL & MADEL (1960, p. 275)

Eucaryoxylon rauscherödense n. sp.

(Fig. 2–8).

Locality: The sand and gravel exposure at Rauscheröd, (Sand- und Kieswerk Rauscheröd ULRICH ALEX GmbH), 2.5 km ENE Ortenburg, 10 km SSE Vilshofen; map 1 : 25000, No. 7445 Ortenburg; fossil finding point: r 45 92 970, h 53 80 700; ca. + 440 m NN.

Stratigraphic position: East Bavarian Molasse, Lower miocene gravel stream of the so-called „Ortenburger Schotter“; Ortenburg Gravel, ca. 15–20 m thick; according to HEISSIG (1997) Mammal Neogene zone MN 4b (Bayer. Geol. Landesamt, 1996).

Age: Lower Miocene gravel stream „Ortenburger Schotter“, as seen at the surface and below ground, was active in Upper Otnang time. It was obviously the first large coarse clastic depositional body of the „Obere Süßwasser Molasse“ to have reached the Molasse basin out of the Alps (BAUBERGER & UNGER et al. 1984, UNGER 1997: 362).

Material: The wood was collected by Dr. F. PFEIL and is deposited in the Bavarian State Collection of Palaeontology and Geology, Munich (PFEIL & WERNER 1991). The original size of the silicified fossil is at present not available due to reorganisation of the State Collection; 10 thin sections, brown, maximum size 2.5 × 4 cm.

2.1. Description

Species diagnosis

Growth rings indistinct. Wood diffuse-porous, vessels solitary and in radial multiples of up to 3, tangential diameter 70–104 µm, thick-walled; perforation plates exclusively simple, vessel element length 130–282 (mean 183) µm, intervessel pits minute, alternate, vessel-ray pits similar. Axial parenchyma apotracheal, partly scanty confluent, wavy parenchyma bands, 1–2–(3) cells wide; barrel-shaped idioblasts in axial strands of 2–10 cells, abundant; axial crystalliferous chains with chambered cells absent. Fibres non-septate, lumen diameter 7–10 µm. Rays heterocellular, 1–2–(3)-seriate, sections with procumbent and upright cells, height 131–565 (mean 131) µm; crystals in ray cells absent; 16–20 rays per mm.

Anatomy

Silicified secondary dicotyledonous wood without bark or pith. Distortion and "folding" of the rays indicates that the wood has been compressed during burial, wood tissue locally deformed and decayed.

Growth rings indistinct; boundaries only slightly marked by differences in tangential vessel diameter between late wood (55 µm) and early wood (100 µm), and by 5–7 radially layers of flattened latewood fibres. Width of growth rings difficult to observe, e.g. 1.6 mm.

Vessel arrangement diffuse-porous, vessels evenly distributed without special arrangement or vessel groupings, solitary (34%) as well as in radial multiples of 2–3, outline in cross section oval to circular. Solitary vessels tangential diameter 70–104 (radial 80–143) µm; multiple vessels flattened, e.g. 2 with tangential diameter 91–109 (radial 162–195) µm, 3 with radial diameter 126 µm, 4 with radial diameter 254 µm; vessel walls locally thick, 8–11 µm. Vessel element length



Fig. 2. Cross section, BSP 1979 XV 18. Xylem tissue partly decayed. Vessel evenly distributed, axial parenchyma apotracheal reticulate, dark rays distorted. $\times 20$. – Microphotographs (Fig. 2–6) A. SELMEIER.

130–282 (mean 183) μm , standard deviation 63 μm , vessel element length difficult to observe due to black deposits. Perforation plates simple, inclination more than 45° , intervessel pits minute (3–4 μm), alternate, ca. 17 pits in a horizontal wall distance of 72 μm , shape of pits oval to circular, aperture slit-like horizontal or rounded, vessel-ray pitting similar to intervessel pitting, thin-walled tyloses present; 9–13 vessels per square millimetre.

Fibres non-septate, in cross section (1)–2–5–(6) rows between 2 rays, in shape circular to oval, diameter 7–10 μm .

Axial parenchyma scanty paratracheal, partly confluent, locally only a few cells associated with the vessels, apotracheal parenchyma bands in more or less concentric tangential lines, also discontinuous, partly wavy, 1–2–(3) cells wide; parenchyma lines regularly spaced, forming a distinctive network with the rays in cross section, radial distance of the bands 51–192 (mean 126) μm , standard deviation 35 μm , parenchyma cells height 26–49 μm , tangential width 20 μm , radial 15 μm ; (4)–5–6–(9) tangential bands per mm measured radially.

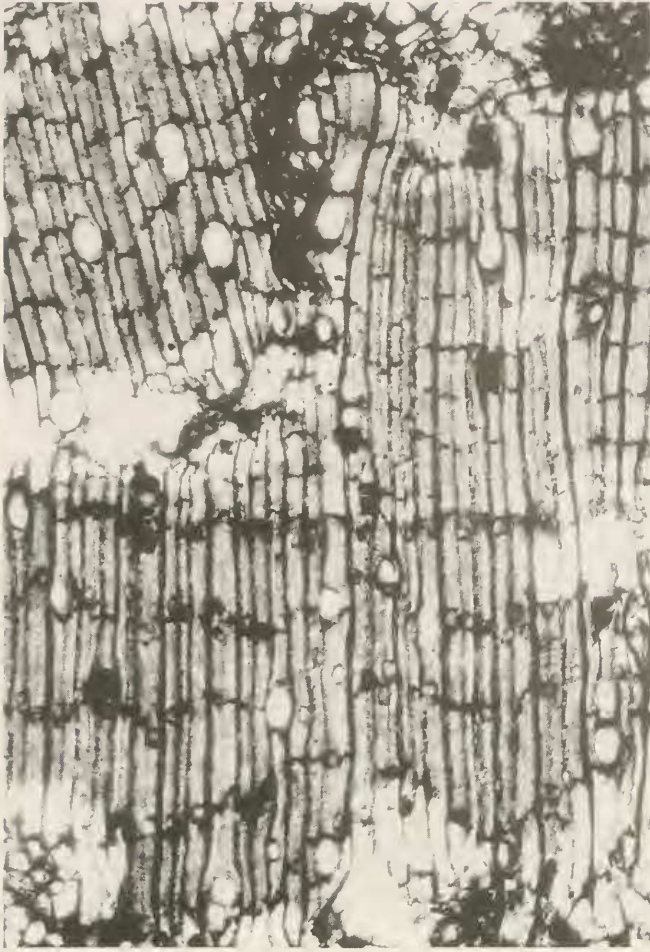


Fig. 3. Cross section, BSP 1979 XV 18. Reticulate pattern between rays and banded parenchyma, idioblasts abundant, mostly in contact with apotracheal parenchyma bands. $\times 40$.

Rays heterocellular, 1–2–(3)-seriate, uniseriate rays ca. 32%, ray height 131–565 (mean 334 μm), standard deviation 99 μm (60 counts); uniseriate rays e.g. 4 upright cells, vertical (23–34 μm), 2-seriate rays have procumbent body cells with some rows of upright marginal cells or marginal cells on one side, upright ray cells height 19–34 μm , tangential width 8–18 μm , radial 23–60 μm , procumbent cells square (10–14 μm) or vertically elongated up to 30 μm ; 16–20 rays per mm in tangential distance.

Mineral inclusions: Crystal-bearing, enlarged barrel-shaped cells (idioblasts), conspicuous even in cross-section, abundant, distributed in the apotracheal parenchyma bands and in the ground tissue, ca. 25 idioblasts per square mm in cross section. Outline of the idioblasts in cross section oval to circular, radial diameter 24–95 (mean 41) μm , standard deviation 8 μm (30 counts), tangential 28–55 μm . In longitudinal sections enlarged cells solitary or in strands of 2–4 – (10) barrel-shaped cells, height 38–182 (mean 105) μm , standard deviation 24 μm (25 counts); crystals solitary, rhomboid, prismatic, size 26–43–(57) μm .

Features (IAWA list, 1989):

- (2) Growth ring boundaries indistinct or absent
- (5) Wood diffuse-porous
- (13) Simple perforation plates
- (22) Intervessel pits alternate
- (24) Intervessel pits minute
- (30) Vessel-ray pits similar to intervessel pits
- (41) Tang. diameter of vessel lumina 50–100 μm
- (47) Vessels per square millimetre 5–20
- (52) Mean vessel element length <350 μm
- (56) Tyloses
- (66) Non septate fibres
- (70) Fibres very thick-walled
- (76) Axial parenchyma diffuse
- (78) Axial parenchyma scanty paratracheal
- (86) Axial parenchyma in narrow bands up to 3 cells wide
- (87) Axial parenchyma reticulate
- (97) Ray width 1 to 3 cells
- (107) Body ray cells procumbent, 2–4 rows of upright cells
- (116) Rays per millimetre >12
- (136) Prismatic crystals present
- (156) Crystals (only) in enlarged cells.

2.2. Affinities

Comparison with extant woods

Affinities were determined by consulting dichotomous keys (Table 1) and reference literature such as BAREFOOT & HANKINS (1882), BRAZIER & FRANKLIN (1961), CARLQUIST (2001), GREGUSS (1959), GREGORY (1994), GROSSER (1977), METCALFE & CHALK (1950), ILIC (1991) and searches of fossil wood databases (WHEELER 1991 a, b). Comparisons were made with sections of extant woods housed in the laboratory of Dr. GROSSER, Institute of Wood Research, Technical University Munich (STERN 1988, Index Xylariorum, p. 229–230). The wood has been described and measurements made in accordance with the International Association of Wood Anatomists' recommendations wherever possible (IAWA Committee of Nomenclature, 1989).

Despite partly insufficient preservation and compression of the structure, this fossil shows a certain number of valuable characters. The most important feature is the predominantly apotracheal parenchyma in numerous 1–3-seriate, more or less regularly spaced bands, forming a network with the rays. This type of parenchyma is found in different genera of Annonaceae, Apocynaceae, Bombacaceae, Casuarinaceae, Ebenaceae, Euphorbiaceae, Juglandaceae, Malvaceae, Rosaceae, Rubiaceae, Sapotaceae, Sterculiaceae and Tiliaceae. In a time-consuming comparison, the whole XylotheC Collection of wood species of the above mentioned 13 families were carefully checked and compared. On examining the fossil thin sections, H. GOTTWALD (Hamburg) considered that the following features confirm an assignment of the fossil wood to the family Juglandaceae, e.g. parenchyma bands distinctly paratracheal, parenchyma locally confluent, vessels often with thin-walled tyloses (personal communication).

Thick-walled vessels, comparatively few vessels, vessel perforations exclusively simple, abundant large barrel-shaped cells with single rhomboid crystals (idioblasts), are present together with tangential wavy parenchyma bands. These characteristic features resemble in microscopic structure the wood of the extant genus *Carya* (25 species), family Juglandaceae.



Fig. 4. Tangential longitudinal section, BSP 1979 XV 18. Rays heterocellular, 1-2-seriate, biseriate sections and uniseriate upright cells. $\times 160$.

The Juglandaceae comprise 4 tribes with 8 extant genera: Juglandae (*Juglans*, *Pterocarya*, *Cyclocarya*), Engelhardiae (*Engelhardia*, *Oreomunnea*, *Alfaroa*), Hicoriae (*Carya*) and Pterocaryae (*Platycarya*). Anatomical features important in distinguishing the 4 extant tribes are presented by MANCHESTER & WHEELER (1993, Table 1). The most fundamental differences involve pith and vessel element perforations. For the identification 6 dichotomous keys are available.

Table 1. Special anatomical dichotomous keys of extant and fossil woods of Juglandaceae.

| Taxa | Extant/Fossil | Genera/Species | References |
|----------------------------------|-------------------|----------------|----------------------------|
| Juglandaceae | Extant | Genera | KRIBS 1927 |
| Juglandaceae | Extant | Genera | MÜLLER-STOLL & MÄDEL 1960 |
| <i>Juglans</i> | Extant | Species | MILLER 1976 |
| Juglandaceae | Extant and fossil | Genera | MANCHESTER 1983 |
| Juglandaceae | Extant and fossil | Genera | DUPÉRON 1988 |
| Juglandaceae, <i>Clarnoxylon</i> | Extant and fossil | Genera | MANCHESTER & WHEELER, 1993 |



Fig. 5. Tangential longitudinal section, BSP 1979 XV 18. Heterocellular rays and seven barrel-shaped idioblasts. $\times 160$.

The 6 dichotomous keys (Table 1) and other anatomical descriptions are a valuable aid on the identification of the present fossil. On the basis of a diagnostic suite of anatomical features the wood can be placed with great certainty in Juglandaceae, tribe Hicoriae, genus *Carya*, form genus *Eucaryoxylon* established for fossil wood. Some families have similar structure, especially in cross-section, e.g. Ebenaceae, but thin-walled tyloses are always absent in that family (MÜLLER-STOLL & MÄDEL-ANGELIEWA 1984).

References:

MANCHESTER (1983): Key 2b; Crystals, when present, in large solitary idioblasts of the axial parenchyma (*Eucaryoxylon*, *Carya*).

MÜLLER-STOLL & MÄDEL-ANGELIEWA (1983): Kristallzellen als große, tonnenförmige Idioblasten einzeln oder zu 2–3 senkrecht übereinander (S. 666). Sobald jedoch Kristallidioblasten vorhanden sind, können sie sicher auf *Carya* bezogen werden und gehören dann zu *Eucaryoxylon*.



Fig. 6. Longitudinal sections, BSP 1979 XV 18. Left ($\times 240$), intervessel pits in tangential view. Right ($\times 250$), barrel-shaped idioblasts with solitary crystals in radial view.

DUPÉRON (1988): Clés d'identification II, B, 2 b; Cristaux dans de grosses cellules en forme de tonneau, isolées ou en files de 2-3 (*Carya* spp.).

Comparison with fossil wood

Fossil woods assigned to the family Juglandaceae are known from a wide range of localities in the Northern Hemisphere. The "Fossil Wood Database" (WHEELER 1991a, b) contains 26 entries for Juglandaceae. MÜLLER-STOLL & MÄDEL (1960) established the 3 genera *Caryojuglandoxylon*, *Eucaryoxylon* and *Pterocaryoxylon* for juglandaceous fossil woods. Additional fossil genera: *Engelhardioxylon* MANCHESTER (1983), *Eucaryoxylon* MÜLLER-STOLL & MÄDEL emend. DUPÉRON (1988: 236), *Rhysocaryoxylon* DUPÉRON (1988) and *Clarnoxylon* MANCHESTER & WHEELER (1993). DUPÉRON (1988) has given a valuable inventory of all fossil woods ascribed to the family Juglandaceae, including G. F. BECK's collection from the western United States. To date, more than 10 fossil woods of the genus *Eucaryoxylon* have been described anatomically.

Table 2. Tertiary woods from Europe attributed to the form genus *Eucaryoxylon* MÜLLER-STOLL & MADEL (1960).

| Fossil name | Locality | Country | References |
|-----------------------------|---------------|---------|-------------------------------------|
| <i>E. crystalloporum</i> | Füzerkomlos | Hungary | MÜLLER-STOLL & MADEL 1960 |
| <i>E. guembelii</i> (FELIX) | Wagenhofen | Germany | MÜLLER-STOLL & MADEL-ANGELIEWA 1983 |
| <i>E. moenanum</i> | Neu-Isenburg | Germany | MÜLLER-STOLL & MADEL-ANGELIEWA 1983 |
| <i>E. budense</i> | Budapest | Hungary | GREGUSS 1969 |
| <i>E. budense</i> | Megyascu | Hungary | GREGUSS 1969 |
| <i>E. boureaui</i> | L'Aquitain | France | DUPÉRON 1977 |
| <i>Eucaryoxylon</i> sp. | Willershausen | Germany | GOTTWALD 1981 |
| <i>Eucaryoxylon</i> sp. | Bergheim | Germany | SELMEIER 1986 |
| <i>E. crystalloporum</i> | Attenfeld | Germany | SELMEIER 1986 |
| <i>E. crystalloporum</i> | Hoyerswerda | Germany | SELMEIER 1990 |
| <i>E. castallanii</i> | Castellane | France | SELMEIER 1995 |
| <i>E. rauscherodense</i> | Rauscheröd | Germany | 2001 |

The most distinctive feature of the fossil from the exposure at Rauscheröd is the abundant presence of large, barrel-shaped idioblasts in axial parenchyma, a consistent feature of *Carya*. Considering the combination of diagnostic features, the fossil wood must be assigned to the genus *Eucaryoxylon* MÜLLER-STOLL & MADEL emend. DUPÉRON (1988), and is named *Eucaryoxylon rauscherodense* n. sp. The epithet *rauscherodense* commemorates the fossil locality Rauscheröd, a famous exposure with abundant woody plant, pollen and vertebrate remains.

The closest similarity exists between *Eucaryoxylon castallanii* (SELMEIER 1990) and the present wood *E. rauscherodense* n. sp. (Table 3).

Table 3. Comparison of two *Eucaryoxylon*-wood remains from Castellane, SE France (Eocene according to label) and Rauscheröd, SE Germany (Lower Miocene); CS-cross section, LS-longitudinal section, TLS-tangential longitudinal section. - *) An anatomical feature which does not exactly correspond with the generic diagnosis for *Eucaryoxylon* MÜLLER-STOLL & MADEL (1960) emend. DUPÉRON 1988.

| Anatomical features | <i>Eucaryoxylon castallanii</i> | <i>E. rauscherodense</i> |
|--------------------------------|---------------------------------|---------------------------|
| Growth rings | indistinct | indistinct |
| Diffuse porous | + | + |
| Vessels solitary, thick-walled | 21%, + | 34%, + |
| Tangential diameter | 55–105 µm | 70–104 µm |
| Perforations simple | + | + |
| *) Intervessel pits minute | 4–5 µm | 4 µm |
| Vessel element length | 315–610 (mean 476) µm | 130–282 (mean 183) µm |
| Thin-walled tyloses | ? | + |
| Vessels per mm | 22–33 | 9–13 |
| Axial parenchyma banded | 1–2 cells wide | 1–2–(3) cells wide |
| Regularly spaced | + | + |
| CS: distinct network | with the rays | with the rays |
| CS: idioblasts | (+) | abundant |
| Idioblasts barrel-shaped | + | abundant |
| *) LS: vertical strands | 7–8 | 2–11, occurrence abundant |
| Crystalliferous strands | abundant | absent |
| Axial chambered cells | 7–22 | absent |
| Strands, vertical height | 185–835 µm | absent |
| LS: single crystals | abundant | absent |
| Rays TLS: 1–2 –(3) seriate | 1–2 | 1–2–(3) |
| *) TLS: heterocellular | + | + |
| *) TLS: different sections | + | + |
| TLS: height | 0.3–0.8–(1.4) mm | 130–568 µm |
| LS: crystals absent | + | + |
| CS: number per mm | 11–14 | 16–20 |

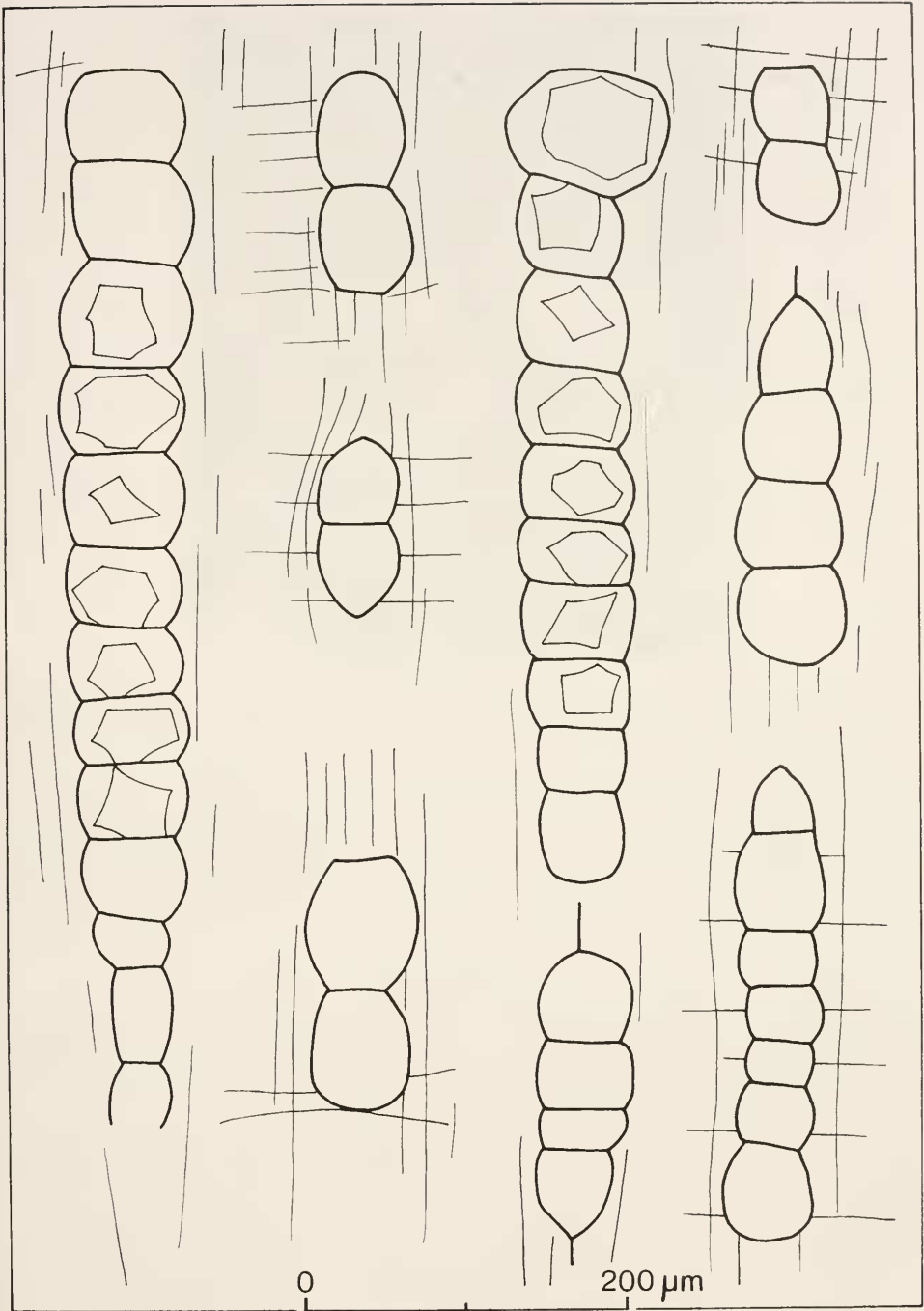


Fig. 7. Longitudinal radial section, BSP 1979 XV 18. Barrel-shaped idioblasts with solitary crystals.

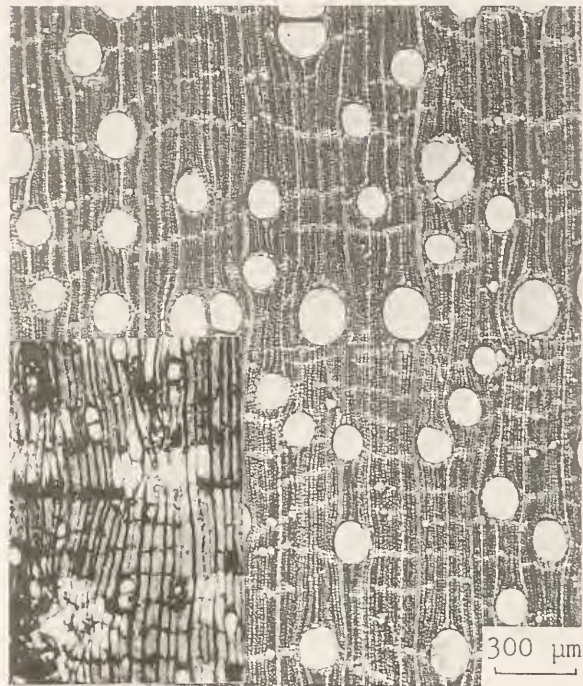


Fig. 8. Cross section. *Carya tonkinensis* LECOMTE (1921) with banded parenchyma and abundant cells with solitary crystals, similar but not identical with *Eucaryoxylon rauscheroedense* n. sp. (left side microphotograph).

Four features marked with *) have already been observed in *Eucaryoxylon castellanii* from SE France (SELMEIER 1995). P. DÉTIENNE, CIRAD-Forêt, Montpellier Cedex, has supported the identification of the Eocene wood from Castellane in the family Juglandaceae (personal communication, 1995). *E. rauscheroedense* and the Eocene wood from Castellane differ in a) minute intervessel pitting, b) distinctly heterocellular ray structure from the generic diagnosis for *Eucaryoxylon* (1960) emend. DUPÉRON 1988.

The length of crystalliferous chains with septate cells is a diagnostic, typical feature of *Juglans* (MÜLLER-STOLL & MÄDEL 1960, MILLER 1976). In the Rauscheröd wood crystalliferous chains with septate chambered cells are absent (Table 3). Also, this fossil does not possess crystals (idioblasts) in the rays, unlike the extinct Juglandaceae *Clarnoxylon* MANCHESTER & WHEELER (1993) or *Engelhardioxylon macrocrystallosum* GOTTWALD (1992).

Crystalliferous cells are not always a consistent feature within all taxa or samples of extant and fossil Juglandaceae. The occurrence of crystals in Juglandaceae (chambered strands, barrel-shaped idioblasts) are obviously dependent on a) the topographic position within the xylem-producing plant individual, b) correlation with traumatic injuries, c) climatic and/or environmental influences. According to the experience of R. B. MILLER (1976), it is apparent that crystals in *Juglans* occur more abundantly in tropical species than in temperate species. Within a taxon that grows in both temperate and tropical zones, the tropical specimens seem to accumulate crystals more frequently.

3. Discussion

More than 70% of the woods identified from the exposure at Rauscheröd and their comparable extant species are exclusively of Old World distribution (GOTTWALD 1997, SELMEIER 1985, 1998, 1999, 2000): genera of Bombacaceae, Ebenaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Lauraceae, Meliaceae, Tiliaceae. With regard to the climatic demands, it must be emphasized that, based on the requirements of comparative extant genera, the most frequently represented fossil genus *Carapoxylon* (Meliaceae; 56 samples) as well as various species of *Bombacoxylon*, *Cedreloxylon*, *Cinnamomoxylon*, *Eudiospyroxylon*, *Euebenoxylon*, *Grewioxylon* and *Homalioxylon*, required tropical temperatures for their growth (GOTTWALD 1997). As far as is known there exists worldwide no other "Lower Miocene locality", Mammal Neogen zone MN 4, with such a large number of Old World and tropically distributed wood genera from a single Tertiary exposure. *Eucaryoxylon rauscherodense* n. sp. shows the closest anatomical similarity in cross section with the extant *Carya tonkinensis* (KRIBS 1928, LECOMTE 1921). This extant *Carya* wood has also, like the above mentioned 8 fossil genera, an Old World distribution.

The Juglandaceae have an excellent fossil record in the Tertiary of the Northern Hemisphere. The fossil record includes both extant and extinct genera (MANCHESTER 1981, 1983). The major radiation of the family occurred during the Lower Tertiary, as recorded in the diversification of pollen (SEITNER 1987), in fruit types and in types of juglandaceous foliage.

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